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RELATIONSHIPS BETWEEN PRODUCTIVITY AND NUTRIENT CIRCULATION WITHIN TWO CONTRASTING SOUTHEASTERN U.S. FLOODPLAIN FORESTS

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Abstract: Patterns of nutrient circulation were examined to provide insight into the controlling mechanisms behind differences in aboveground net primary production (ANPP) among floodplain forest types. Geochemical and biogeochemical contrasts typical of many riverine forests are exemplified by the floodplains of the Satilla and Altamaha Rivers, blackwater and redwater river systems, respectively, located in Georgia, USA. Since floodplains possess high microtopographic variation, measurement plots were established to cover a range of topographic positions across both floodplains. Given the low nutrient and sediment loads that are characteristic of blackwater rivers, we hypothesized that the Satilla floodplain (SAT) would have lower ANPP and more efficient nutrient use efficiency (NUE). While both floodplains had similar amounts of litterfall production, the Altamaha floodplain (ALT) had greater stem production and, therefore, higher rates of ANPP. On the SAT, the relationship between litterfall mass and litterfall phosphorus (P) content, high P NUE, and high P resorption proficiency suggested that P was the primary limiting nutrient. While (N) circulation patterns were similar for the floodplains, ALT floodplain litterfall N/P ratios and N NUE suggested that N limitation was paramount there. Patterns of base cation circulation on the SAT indicated low calcium and potassium circulation and higher NUE of these elements compared to the ALT. In contrast, the Altamaha floodplain displayed low magnesium (Mg) circulation and high Mg NUE. Differences in P circulation and P NUE appeared to have the largest influence on ANPP between these eutrophic (ALT) and oligotrophic (SAT) floodplain forests. Furthermore, differences in base cation circulation and NUE suggested that biogeochemical distinctions between these two floodplain types could be made on the basis of base cation availability.

Key Words: aboveground net primary production, calcium, floodplain forests, nitrogen, nutrient use efficiency, magnesium, phosphorus, potassium, resorption proficiency, southeastern United States

INTRODUCTION

Floodplain forests are distinguished as oligotrophic or eutrophic as a result of the influences of landscape position, mineralogy, and hydrology within watersheds (Lugo et al. 1990, Sharitz and Mitsch 1993). In the southeastern United States, these river systems are commonly referred to as redwater and blackwater rivers, respectively (Wharton 1978, Wharton et al. 1982). Redwater rivers are characterized by high nutrient loads derived from weathering and leaching of parent materials of Piedmont soils (Sharitz and Mitsch 1993), resulting in highly productive floodplain forests (Wharton et al. 1982). In contrast, low-gradient blackwater rivers originate in the Coastal Plain where their associated floodplain forests are thought to be less productive due to lower suspended sediments and dissolved inorganics in their river waters (Wharton et al. 1982). Furthermore, many blackwater rivers are Coastal Plain tributaries of their larger redwater river counterparts.

Given the differences in nutrient inputs, questions arise regarding patterns of nutrient circulation and productivity of their associated floodplain forests. Greater potential for high nutrient availabilities in floodplain soils suggest that nutrient deficiencies may not be critically limiting to aboveground net primary production (ANPP) within riverine forests (Lugo et al. 1990). Because variation in ANPP ranges from 2–20 Mg ha^{-1} yr^{-1} (Conner 1994), however, it is unclear how differing inputs of various nutrients influence ANPP in southeastern US floodplain forests.

Globally, forest productivity is primarily limited by nitrogen (N) and secondarily by phosphorus (P) availability (Vitousek and Howarth 1991), and the circulation of these nutrients in forest systems can be defined as either ''efficient'' or ''inefficient'' (Vitousek 1984). Forests with efficient nutrient circulation patterns have relatively large amounts of carbon (C) fixed per unit of nutrient uptake. Thus, efficient nutrient circulation patterns suggest greater nutrient limitations than inefficient nutrient circulation patterns that may reflect adequate or surplus supply (Vitousek 1982, Vitousek 1984).

In response to these limitations, resorption of nutrients from senescing foliage could increase nutrient conservation (Aerts 1996, Killingbeck 1996) by reducing dependence on soil nutrient supplies (Jonasson and Chapin 1985). Additional insight into nutritional influences on ANPP may be found by examining the balance of N and P within wetland vegetation since nitrogen/phosphorus (N/P) ratios may indicate the degree to which either N or P constrains ANPP (Koerselman and Meuleman 1996). For wetland forests in particular, Lockaby and Conner (1999) have suggested that litterfall N/P ratios have predictive value regarding N and P imbalance and limitations.

While many studies have focused on patterns of N and P circulation within temperate and tropical floodplain forests (Vitousek 1982, Vitousek 1984, Lugo et al. 1990, Lockaby and Conner 1999), further insight may be gained by examining patterns of base cation circulation. Nutrient limitations to ANPP may involve multiple elements (Cuevas and Medina 1986, Gerrish et al. 1988, Reich et al. 1995), so base cation availability could regulate levels of floodplain forest production similar to that observed in some temperate forests (McLaughlin and Wimmer 1999).

The blackwater Satilla River originates in the sandy Georgia Coastal Plain and has low nutrient and sediment loads. Conversely, the redwater Altamaha River lies in the clayey Georgia Piedmont and carries higher nutrient and sediment loads. Since these two river systems are very different biogeochemically, the relationships between nutrient circulation and ANPP may also differ. Specifically, we hypothesized that the blackwater Satilla floodplain forest would have lower rates of ANPP and nutrient circulation in litterfall, resulting in more efficient nutrient use. We examined these relationships by measuring ANPP, nutrient return in litterfall, nutrient resorption proficiency, and nutrient use efficiency (NUE) in these two contrasting riverine forests.

METHODS

River and Study Site Descriptions

The Satilla River and Floodplain. The watershed of the low gradient, blackwater Satilla River system lies entirely within the lower Coastal Plain. Consequently, low sediment and nutrient loads dominate (Table 1). Satilla waters possess high dissolved organic C content and low pH (Beck et al. 1974, Cai and Wang 1998).

Table 1. Watershed area, discharge, and nutrient loads for the Satilla and Altamaha Rivers, Georgia, USA.

	Satilla River	Altamaha River
Watershed area (ha^2)	914,313	22,957,647
Average Discharge (m^3 s^{-1})	15.0	166.3
Suspended sediment (kg ha^{-1} yr^{-1})	11.0	57.1
Total organic C (kg ha^{-1} yr^{-1})	12.7	11.5
Total N (kg ha^{-1} yr^{-1})	0.6	1.0
Total P (kg ha^{-1} yr^{-1})	0.07	0.07
Total Ca (kg ha^{-1} yr^{-1})	2.3	20.0
Total K (kg ha^{-1} yr^{-1})	0.1	2.7
Total Mg (kg ha^{-1} yr^{-1})	1.4	2.8

† Data for the Satilla and Altamaha Rivers calculated from US Geological Survey.

The Satilla River study site (SAT) was located in Brantley Co., Georgia (31°23′N, 81°88′W). At the site, nine circular plots (10-m diameter) covering three microsite types (n = three per type) were established based on differences in soils. Microsite types were classified as moderately poorly drained (MPD), intermediate (INT), and very poorly drained (VPD). Soils of MPD and INT microsites were Kinston series (fine-loamy, siliceous, Typic Fluvaquents). Redoximorphic features (i.e., mottles, gleying, etc.) were observed in the field at depths of >30 cm for MPD microsites and at <15 cm depths for INT microsite soils. Soils of VPD microsites were classified as Humaqueptic Fluvaquents, which are similar to the Kinston series but possessed more organic matter throughout their soil profile to a 1-m depth. Redoximorphic features were found at depths of <10 cm.

At all microsite types, sweetbay (*Magnolia virginiana* L.), black tupelo (*Nyssa sylvatica* Marshall var. *sylvatica*), red maple (*Acer rubrum* L.), laurel oak (*Quercus laurifolia* Michx.), and sweetgum (*Liquidambar styraciflua* L.) were present. Pondcypress (*Taxodium distichum* var. *nutans* [Ait.] Sweet) was also present at the INT and VPD microsites. Across all microsites, mid-story species included ti-ti (*Cyrilla racemiflora* L.) and buckwheat-tree (*C. monophylla* L.), while the understory consisted of Elliott blueberry (*Vaccinium elliottii* Chapm.) and blue palm (*Sabal minor* (Jacquin) Persoon). Increment cores taken from laurel oak trees within all sample plots (one core per tree) indicated a stand age for the dominant canopy of approximately 70 years.

The Altamaha River and Floodplain. The Altamaha River watershed begins in the Piedmont, and therefore, river waters are high in sediment and other nutrients (Table 1). Altamaha River waters also possess higher carbonate content and pH compared to the Satilla River (Beck et al. 1974, Cai and Wang 1998).

The Altamaha River study site (ALT) is located within the Griffin Ridge Wildlife Management Area, Long Co., Georgia (31°68′N, 81°82′W). Similar to the SAT floodplain site, nine circular plots (10-m diameter) were established on somewhat poorly drained (SPD), intermediate (INT), and poorly drained (PD) microsite types (n = three per type). One SPD plot was not used in the analyses since it was found to differ in soil type and species composition compared to the other two SPD microsite plots. Soils of SPD, INT, and PD microsites were the Ocilla series (loamy, siliceous, Aquic Arenic Paleudults), Osier series (siliceous, Typic Psammaquents—redoximorphic features at soil depths >10 cm), and Bibb series (coarse-loamy, siliceous, Typic Fluvaquents—redoximorphic features at soil depths <10 cm), respectively.

The vegetation of the ALT floodplain consisted primarily of laurel oak, red maple, and sweetgum, which were found across all three microsite types. On INT and PD microsites, overcup oak (*Q. lyrata* Walt.), ogeechee tupelo (*N. ogeche* Bartr. ex Marsh.), and water tupelo (*N. aquatica* L.) were also present. Baldcypress (*T. distichum* [L.] Rich.) and pondcypress grew only in the PD microsites. The INT and PD microsites also lacked woody and herbaceous understories, but on the drier SPD microsites, blue palm was often present. Laurel oak increment cores, taken across all plots, indicated a stand age for the dominant canopy of approximately 75 years.

Soil Nutrients

Soils were sampled bimonthly from April to October 1999 for plots of both floodplains. Three soil cores from each plot were taken at random using a 5-cm-diameter bucket auger to a depth of 10-cm. In the lab, soils were air dried and sieved to remove roots and other organic materials. Individual soil cores were then analyzed separately for total C, percent organic matter, total N, extractable-P, and exchangeable-calcium (Ca), potassium (K), and magnesium (Mg). Percent organic matter, as well as total C and N, were determined by dry combustion (Nelson and Sommers 1996). Inductively coupled argon plasma (ICAP) analysis (Jarrell-Ash 9000, Genesis Laboratory Systems Inc., Grand Junction, CO) was used to determine soil extractable-P and exchangeable base cations after extraction with a double-acid (0.05 N HCl and 0.025 N H_2SO_4) reagent (Hue and Evans 1986).

Aboveground Net Primary Production

From November 1998 to 2000, litterfall was collected at monthly intervals from three randomly located 0.25-m^2 traps per plot. Litter traps were constructed on a styrofoam base that would rise during flood events and also possessed a nylon mesh screen that was raised 5-cm above the litter trap base to prevent inundation. For each individual trap, litterfall was sorted into leaf, reproductive and woody debris components, oven-dried for 48 hr at 70°C, and weighed. Monthly litterfall weights for each plot were then averaged.

Basal area for plots of both floodplains was determined in July 1998 using a base-10 prism. Stem production for species on both floodplains was determined from annual changes in stem biomass derived from allometric equations that were based on diameter at breast height (dbh) and total height as independent variables (Clark et al. 1985). Annual changes in wood biomass for *Taxodium* spp. were calculated using allometric equations with dbh as the only independent variable (Scott et al. 1985). Stem diameter was measured above the butt swell for large trees. For all plots, dbh (~1.3 m) and total height of all stems with >10-cm diameters were measured annually using a diameter tape and clinometer, respectively. Trees were numbered with aluminum tags and used to mark the location of DBH measurements. Contribution of wood production from <10-cm-diameter stems was assumed to be a relatively small fraction of ANPP since growth rates of saplings are typically low due to the combined effects of low light availability and flooding (Brinson 1990). While Elliott blueberry (*Vaccinium elliottii* Chapm.) was common in the shrub stratum of the SAT floodplain, this species was not an overwhelming component of the understory. Schlesinger (1978) concluded that shrub production accounted for 15% of the above-water community production, or approximately 100 g m^{-2} yr^{-1}, within a cypress stand of the Okefenokee Swamp. However, this estimate unlikely reflects understory annual production on the SAT floodplain accurately due to differences in species composition, soils, flooding, and canopy leaf area. Therefore, total ANPP was calculated as the sum of annual litterfall, which included litterfall produced by understory shrubs and trees with diameters less than 10 cm, and annual stem production. Furthermore, woody debris collected in the litterfall traps was not included in ANPP estimates because all wood production was accounted for by estimation of whole-tree wood biomass.

Litterfall Nutrients

Monthly litterfall collections (i.e., leaf and reproductive components) from each plot (n = three per plot) were ground to pass a 20-mesh sieve following oven drying at 70°C for 48 hrs. Total C and N were determined using a Perkin Elmer Series II CHNS/O Analyzer 2400 (Perkin Elmer Corp., Norwalk, CT). Total P was determined using the vanadomolybdate procedure on an HCl extract following dry ashing at 500°C for 4 hr (Jackson 1958). Calcium, K, and Mg were also determined from samples that were dry-ashed at 500°C for 4 hr, taken up in a double-acid extractant (1 N HCl and 1 N HNO_3), and measured using ICAP analysis (Hue and Evans 1986). Percent lignin was determined using procedures from Van Soest and Wine (1968).

Nutrient Resorption

Nutrient resorption was calculated as resorption proficiency, the terminal nutrient concentration in senesced leaves (Killingbeck 1996), and was expressed as the concentration (%) of N or P. Resorption of N and P was determined at the individual species and at the community (i.e., microsite) levels. Comparisons of resorption proficiency at the species level using senesced foliage of laurel oak and red maple allowed for direct comparison of site influences on N and P resorption within and between floodplains. Senesced foliage was collected in November 1999 and 2000 from numbered trees, with the total number of trees sampled for the SAT numbering 18 (n = nine trees per species) and for the ALT numbering 16 (n = eight trees per species). A single trap was placed under each tree to collect the abscised foliage.

At the community level, resorption proficiency was determined using leaves collected in litterfall traps of each plot during the period of peak litterfall (October–January), thus accounting for differences in temporal patterns of leaf senescence across microsites of both floodplains (Lockaby and Walbridge 1998). Use of a community level index accounted for potential differences in topographic position and species composition that may influence spatial patterns of N and P circulation and resorption. Leaves were dried at 70°C for 48 hrs, weighed, ground to pass a 20-mesh sieve, and analyzed for total N and P.

Live Foliage Nutrients

Live foliage was also collected from the upper canopy of laurel oak and red maple trees during the mid-summer months (July–August 1999 and 2000) from one tree of each species within plots of both floodplains. Therefore, the total number of trees sampled for live foliage on the SAT and ALT floodplains numbered 18 and 16 trees, respectively. Collected foliage was oven dried at 70°C for 48 hrs, ground to pass a 20-mesh sieve, and analyzed for total N and P.

Statistical Analyses

The plot layout for each floodplain was a completely randomized design with treatments covering three microsite types that differed in topographic position and soils on both floodplains. Plots within each microsite category were non-contiguous given the heterogeneous nature of soils, vegetation, and hydrology within both floodplains. All data analyses were performed using SAS (SAS Institute 1996). Mean comparisons between floodplains for soil nutrients, ANPP indices, litterfall nutrients, and resorption proficiencies were performed using paired *t* tests and considered significant at the $P < 0.05$ level. We used the GLM procedure to test relationships among litterfall mass and nutrient response variables (i.e., a test for heterogeneity of slopes) as described by Freund et al. (1986) for solving linear models within the GLM procedure. For both floodplains, nutrient use efficiency (NUE) diagrams were created after plotting litterfall dry mass/nutrient ratios against litterfall nutrient content (Vitousek 1982).

RESULTS

Soil Nutrients

Soil total C and N pools for the SAT and ALT floodplains were similar (Table 2). However, soil extractable-P concentrations for the SAT significantly exceeded levels of the ALT floodplain by 4.3 mg kg^{-1}. Soil base cation availability was greater for the ALT floodplain soils, particularly for exchangeable-Ca and K and to a lesser extent exchangeable-Mg (Table 2).

Aboveground Net Primary Production

Basal area and mean overstory height for the SAT floodplain averaged 7.7 m^2 ha^{-1} and 14.1 m compared to 25.1 m^2 ha^{-1} and 20.7 m, respectively, for the ALT floodplain. Two-year mean litterfall production within the SAT and ALT floodplains did not differ (Table 2). For the SAT floodplain, stem production (3.6 Mg ha^{-1} yr^{-1}) was significantly lower than that observed for the ALT floodplain (5.2 Mg ha^{-1} yr^{-1}). Total ANPP for the ALT floodplain significantly exceeded that of the SAT floodplain by 1.9 Mg ha^{-1} yr^{-1} (Table 2).

Litterfall Nutrients and Relationships with Productivity

Amounts of N returned in litterfall for the SAT floodplain were slightly greater (2.8 kg N ha^{-1} yr^{-1})

Table 2. Mean comparisons for soil variables, ANPP, litterfall nutrients, resorption proficiency, and live foliage N and P concentrations on the Satilla and Altamaha River floodplains, Georgia, USA.

	Satilla	Altamaha	Prob > |T|
Soils			
Total C	2.5 ± 0.5	2.6 ± 0.5	0.90
Total N	0.10 ± 0.02	0.11 ± 0.02	0.90
Extractable-P (mg kg^{-1})	9.3 ± 0.4	5.5 ± 0.3	<0.0001
Exchangeable-Ca (mg kg^{-1})	101 ± 7	460 ± 25	<0.0001
Exchangeable-K (mg kg^{-1})	56 ± 3.2	94 ± 5.4	<0.0001
Exchangeable-Mg (mg kg^{-1})	80 ± 4.2	97 ± 4.8	0.008
Production (2-year mean)			
Litterfall (Mg ha^{-1} yr^{-1})	4.8 ± 0.1	5.0 ± 0.1	0.18
Stem (Mg ha^{-1} yr^{-1})	3.6 ± 0.5	5.2 ± 0.6	0.05
Total ANPP (Mg ha^{-1} yr^{-1})	8.3 ± 0.5	10.2 ± 0.6	0.03
Litterfall Nutrients (2-year mean)			
N (kg ha^{-1} yr^{-1})	39.8 ± 2.2	37.0 ± 1.4	0.29
P (kg ha^{-1} yr^{-1})	4.0 ± 0.2	8.0 ± 0.4	<0.0001
Ca (kg ha^{-1} yr^{-1})	54.0 ± 2.1	65.0 ± 2.7	0.003
K (kg ha^{-1} yr^{-1})	8.9 ± 0.3	13.0 ± 0.8	<0.0001
Mg (kg ha^{-1} yr^{-1})	13.6 ± 0.6	10.5 ± 0.4	0.0002
C/N ratio	67.3 ± 2.8	65.6 ± 3.3	0.69
N/P ratio	9.7 ± 0.2	6.1 ± 0.1	0.001
C/P ratio	563.8 ± 9.7	322.8 ± 4.7	<0.0001
Lignin/N	32.3 ± 0.7	36.2 ± 1.0	0.007
Lignin/P	427 ± 12	222 ± 8	<0.0001
N Resorption Proficiency (2-year mean)			
Red maple (%)	0.54 ± 0.04	0.42 ± 0.02	0.005
Laurel oak (%)	0.50 ± 0.02	0.43 ± 0.04	0.13
Litterfall (%)	0.77 ± 0.06	0.71 ± 0.03	0.33
P Resorption Proficiency (2-year mean)			
Red maple (%)	0.09 ± 0.004	0.13 ± 0.007	<0.0001
Laurel oak (%)	0.07 ± 0.007	0.11 ± 0.01	0.006
Litterfall (%)	0.07 ± 0.002	0.14 ± 0.004	<0.0001
Live Foliage (2-year mean)			
N (mg kg^{-1})	14000 ± 300	16000 ± 300	0.0001
P (mg kg^{-1})	1600 ± 50	2200 ± 90	<0.0001

† Values are means ± 1 SE.

than the ALT floodplain, but differences were not significant (Table 2). Relationships between litterfall mass and litterfall N content for both floodplains were plotted across both sample years (Figure 1a). Between both floodplains, differences in the relationships between litterfall mass and N content were small, with the relationship for the SAT floodplain ($r^2 = 0.46$, $P = 0.002$) being slightly more variable than that of ALT floodplain ($r^2 = 0.52$, $P = 0.002$). Furthermore, the similar slopes of the regression lines ($P = 0.30$) suggest similar relationships between N circulation and ANPP for both floodplains.

The amount of P returned in litterfall for the SAT floodplain was significantly lower than that of the ALT floodplain by an average of 4.0 kg ha^{-1} yr^{-1} (Table 2). Relationships between litterfall mass and litterfall P content on the SAT ($r^2 = 0.86$, $P = 0.0001$) and ALT ($r^2 = 0.35$, $P = 0.02$) floodplains, suggests greater P limitation to production on the former (Figure 1b). The relationship between litterfall mass and P content on the SAT floodplain indicates that productivity there seems to be strongly related to P availability. Even though a significant relationship for P was observed on the ALT floodplain, the differing regression line slopes ($P = 0.0007$) suggest that changes in P availability are closely linked to greater changes in productivity on the SAT compared to the ALT floodplain.

Litterfall C/N ratios were similar for both floodplains. However, litterfall N/P, C/P, and lignin/P ratios were all significantly lower for the ALT floodplain

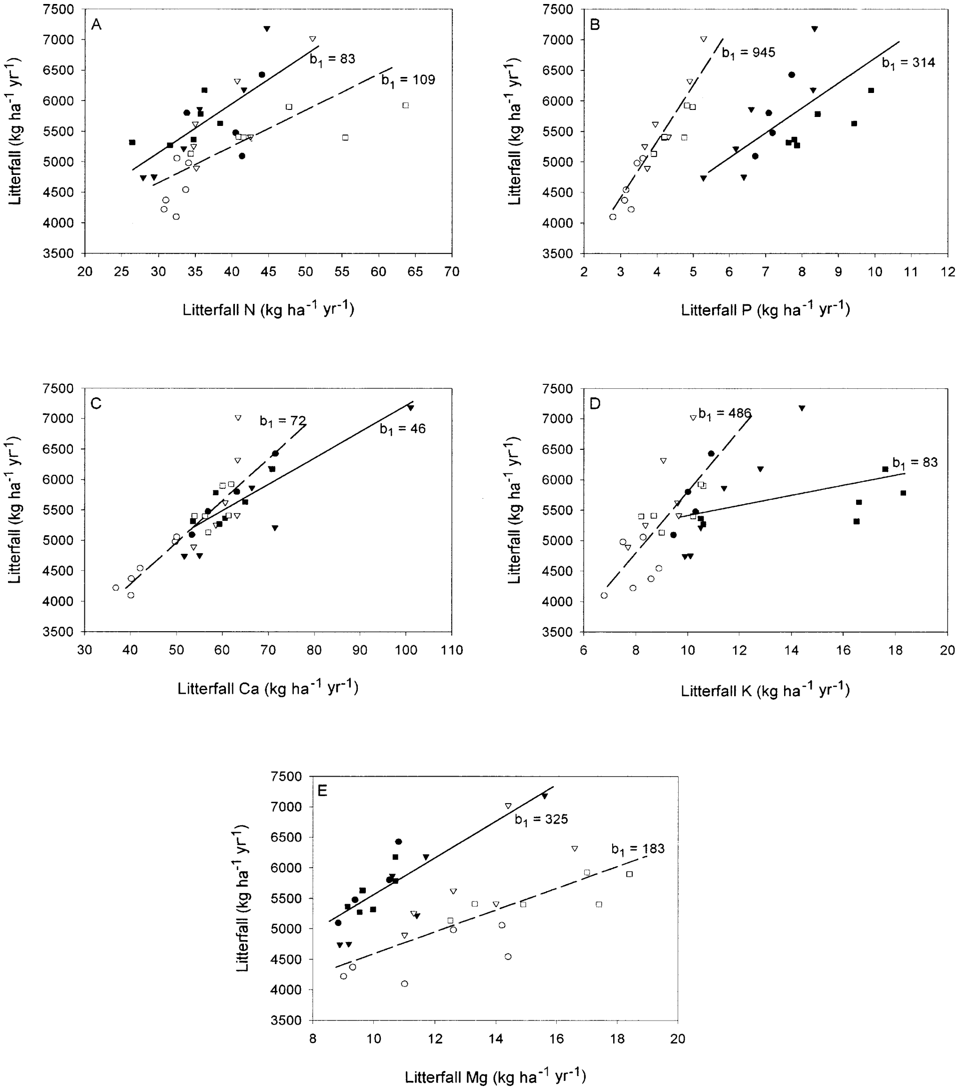

Figure 1. Litterfall mass (kg ha^{-1} yr^{-1}) plotted against litterfall nutrient contents (kg ha^{-1} yr^{-1}) for the Satilla (MPD microsites = open circles; INT microsites = open triangles; VPD microsites = open squares) and Altamaha (SPD microsites = filled circles; INT microsites = filled triangles; PD microsites = filled squares) River floodplains, Georgia, USA for 1999 and 2000. Dashed lines show linear regressions for the Satilla and solid lines for the Altamaha River floodplains. The b_1 coefficients are the slopes of the respective regression lines. Nitrogen (A); Phosphorus (B); Calcium (C); Potassium (D); Magnesium (E).

(Table 2). In contrast, lignin/N ratios for the ALT floodplain were significantly larger than those found for the SAT floodplain (Table 2).

Amounts of Ca returned in litterfall on the ALT floodplain were significantly greater than those on the SAT floodplain by 11 kg ha^{-1} yr^{-1} (Table 2). Relationships between litterfall mass and litterfall Ca content were similar for the SAT and ALT floodplains ($r^2 = 0.76$, $P = 0.0001$ and $r^2 = 0.75$, $P = 0.0001$, respectively, Figure 1c). However, the slopes of both lines differed significantly ($P = 0.04$) suggesting that Ca availability on the SAT floodplain is more sensitive to production than is the case on the ALT floodplain.

Litterfall K content for the SAT and ALT floodplains differed significantly (8.9 vs. 13.0 kg ha^{-1} yr^{-1}, Table 2). On the ALT floodplain, no relationship between litterfall mass and litterfall K content was evident ($r^2 = 0.16$, $P = 0.12$, Figure 1d) suggesting that K availability does not constrain production there. In contrast, the significant relationship for the SAT floodplain ($r^2 = 0.51$, $P = 0.0009$) suggests that K availability may limit productivity on this floodplain.

In contrast to the patterns observed for Ca and K returned in litterfall, the amount of Mg returned in litterfall on the SAT floodplain was significantly greater than that found for the ALT floodplain (Table 2). Significant relationships between litterfall mass and litterfall Mg content on the ALT floodplain ($r^2 = 0.45$,

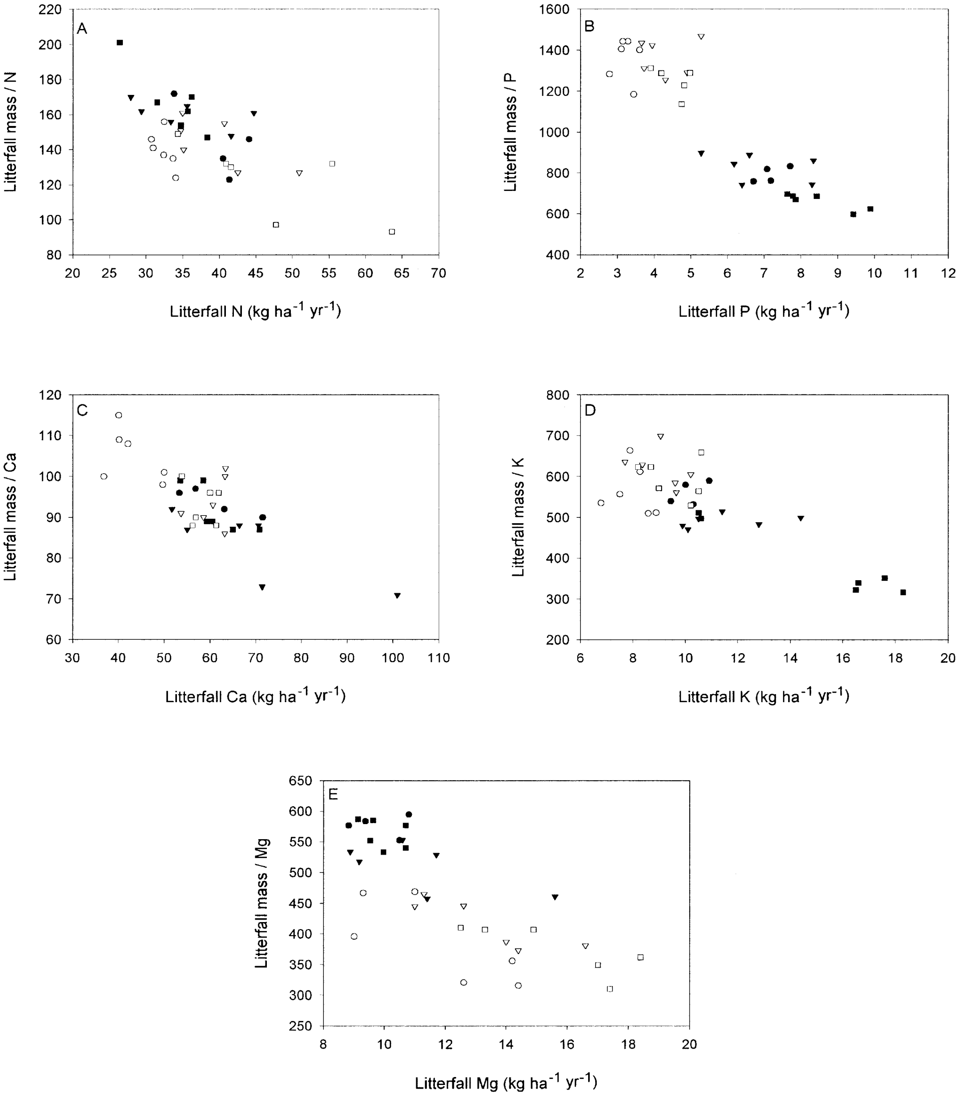

Figure 2. Litterfall mass/nutrient ratio of litterfall plotted against litterfall nutrient contents (kg ha^{-1} yr^{-1}) for the Satilla (MPD microsites = open circles; INT microsites = open triangles; VPD microsites = open squares) and Altamaha (SPD microsites = filled circles; INT microsites = filled triangles; PD microsites = filled squares) River floodplains, Georgia, USA for 1999 and 2000. Nitrogen (A); Phosphorus (B); Calcium (C); Potassium (D); Magnesium (E).

P = 0.003) and SAT floodplain (r^2 = 0.70, P = 0.0001) were observed (Figure 1e). Even though the difference in slope between the regression lines was not significant (P = 0.11), the relationship between litterfall mass and litterfall Mg content, as well as decreased Mg circulation in litterfall, suggests that Mg availability may constrain production on the ALT floodplain.

Nutrient Use Efficiency

To examine nutrient use efficiency (NUE) between the floodplains and among microsite types, we calculated the ratio of litterfall production to litterfall nutrient content across both years. Calculation of NUE indices revealed that N circulation within the SAT floodplain was, in general, less efficient (Figure 2a). Inefficient N circulation patterns were particularly evident for the VPD and, to some extent, the PD microsites of the SAT, while the drier MPD microsites appeared to circulate N more efficiently. Circulation of P in litterfall was dramatically different between both floodplains and indicated that the SAT floodplain was much more efficient at cycling P (Figure 2b). The narrow range of litterfall P content (3–5 kg ha^{-1} yr^{-1}) for the SAT floodplain compared to the ALT (5–10 kg ha^{-1} yr^{-1}) resulted in high P NUE on the former. Differences in litterfall P content across the ALT floodplain did not result in large differences in patterns of P NUE among microsites.

Differences in the efficiencies of Ca usage for both floodplains were small (Figure 2c). However, the drier SAT floodplain microsites appeared to circulate Ca very efficiently compared to the INT and VPD microsites. Additionally, K NUE for the SAT floodplain was higher compared to the inefficient circulation observed for the ALT (Figure 2d). Considerable variation in Mg NUE was evident within vegetation of the SAT floodplain, while the relationship between Mg circulation and litterfall was much clearer for the ALT (Figure 2e).

Resorption Proficiency

Laurel oak N concentrations in senesced foliage did not differ significantly between floodplains (Table 2). However, red maple senesced foliage N concentrations were significantly lower on the ALT (0.42%) compared to the SAT floodplain (0.54%). Senesced foliage P concentrations on the SAT floodplain for red maple and laurel oak were significantly lower (0.09 and 0.07%, respectively) than those concentrations found for the same ALT floodplain species (0.13 and 0.11%, respectively).

At the community level, litterfall N concentrations did not differ significantly between the two floodplains (Table 2). By contrast, SAT floodplain litterfall P concentrations (0.07%) were significantly lower than litterfall P concentrations on the ALT floodplain (0.14%).

DISCUSSION

Overall, ANPP for both the SAT and ALT floodplains are in the ranges reported for riverine forests of the southeastern US (Megonigal et al. 1997) and follow patterns suggested by Lockaby and Conner (1999), who found that ANPP of redwater river floodplains often exceeds levels of blackwater river floodplains. For the SAT floodplain, litterfall and stem growth accounted for approximately 60 and 40% of ANPP, respectively, compared to 52 and 48%, respectively on the ALT floodplain. Litterfall production within both the SAT and ALT floodplains is intermediate among those reported for several other riverine forest communities of the southeastern US (Table 3). Litterfall production within the SAT floodplain was variable among microsites, with the drier (MPD) microsite type having the lowest levels of production during both years (Figure 1). Litterfall production was similar among microsites and between years for the ALT floodplain. Given similar levels of litterfall production for both floodplains, high stem production on the ALT floodplain ultimately drove the higher levels of ANPP observed there.

Table 3. Litterfall mass, litterfall nutrient contents, and nutrient use efficiency for temperate riverine and depressional wetland forests.

		Litterfall											
			Nutrient contents					Nutrient Use Efficiency†					
Location	Forest Type	Dry Mass	N	P	Ca	K	Mg	N	P	Ca	K	Mg	Reference
		Mg ha^{-1}	--------- kg ha^{-1} yr^{-1} ----------										
Satilla River, GA	Floodplain forest (blackwater)	5.3	40	4.0	54	9.0	14	133	1325	698	589	379	This study
Altamaha River, GA	Floodplain forest (redwater)	5.7	37	8.0	65	13	11	154	713	88	439	518	This study
Flint River, GA	Floodplain forest (redwater)	6.2	33	4.1	—	—	—	188	1512	—	—	—	Clawson et al. 2001
Tar River, NC	Floodplain forest (redwater)	6.4	73	5.4	45	21	17	88	1185	142	305	377	Brinson et al. 1980
Lower Three Runs Creek, SC	Floodplain forest (blackwater)	6.7	34	—	67	16	18	197	—	100	419	372	Shure and Gottschalk 1985
Sangamon River, IL	Floodplain forest (redwater)	4.9	83	8.1	87	22	14	59	604	56	223	350	Peterson and Rolfe 1982
Mississippi River, MS	*P. deltoides* plantation	4.7	89	8.0	109	69	14	53	588	43	668	335	Nelson et al. 1987
Dismal Swamp, VA	Maple-gum stand (depressional)	5.4	62	3.4	59	17	17	87	1588	92	318	318	Gomez and Day 1982
Dismal Swamp, VA	Cypress stand (depressional)	5.3	66	4.5	61	16	17	80	1178	87	331	312	Gomez and Day 1982
Dismal Swamp, VA	Cedar stand (depressional)	5.1	62	3.4	70	9.0	13	82	1500	73	567	392	Gomez and Day 1982
Dismal Swamp, VA	Hardwood stand (depressional)	4.6	52	2.3	60	12	14	89	2000	77	383	329	Gomez and Day 1982
North central, FL	Cypress dome (depressional)	4.8	—	1.6	57	3.3	8.0	—	3000	84	1454	600	Odum and Ewel 1979
Okefenokee Swamp, GA	Cypress stand (depressional)	3.3	27	1.3	39	3.4	6.0	122	2539	85	971	550	Schlesinger 1978

† Nutrient use efficiency refers to the ratio of litterfall production to litterfall nutrient content for each study.

For both floodplains, litterfall mass was not closely coupled with N circulation, and the amounts of N circulated in the litterfall of both was similar to estimates reported for other Southeastern wetland forests (Table 3). This trend reflects the similar soil N pools, as well as similar patterns of N resorbed from senesced foliage of both floodplains. Resorption of N is highly proficient in vegetation that reduces N concentrations in its senesced leaves below 0.7% (Killingbeck 1996). For the same two species on both floodplains, senesced foliage N concentrations indicated proficient N resorption (Table 2). This pattern was also evident for litterfall N concentrations of both floodplains, albeit to a slightly lesser degree of proficiency.

While soils on both floodplains displayed similar levels of total N, extractable-P on the SAT floodplain was greater. Increased soil P levels for blackwater floodplain forests of Georgia were also observed by Wharton et al. (1982). Lower extractable-P for ALT floodplain soils may have resulted from P sorption onto clay particles (Mitsch and Gosslink 2000), since most of the sediment deposited by alluvial redwater rivers consists of fine-grained clays and silts (Sharitz and Mitsch 1993). Precipitation of insoluble iron and aluminum phosphates (Lockaby and Walbridge 1998) is also a possible mechanism resulting in decreased P availability on the ALT floodplain.

In spite of greater extractable soil P on the SAT, biotic indications of P deficiency there are more numerous than on the ALT floodplain. Circulation of P in litterfall on the SAT floodplain was low compared to other Southeastern floodplain forests, indicating that the SAT floodplain vegetation circulates P efficiently (Table 3). Efficient P circulation was also evident when examining the patterns of P resorption from senesced foliage. Vegetation resorption of P is moderately proficient when concentrations in senesced foliage are reduced below 0.08% and highly proficient when concentrations are lower than 0.05% (Killingbeck 1996). For both laurel oak and litterfall on the SAT floodplain, moderately proficient P resorption is indicated, while P resorption for red maple was incomplete (Table 2). Conversely, P resorption was inefficient for vegetation on the ALT floodplain. These indices suggest that N is secondary to P in constraining productivity within the oligotrophic SAT floodplain forest.

Additional evidence for P limitation on the SAT floodplain can be found by examining live foliage P concentrations. The average P concentrations in live foliage for both floodplains fall on either side of 2000 mg kg^{-1} (Table 2), a value suggested as a critical concentration for some deciduous tree species (Mills and Jones 1996, Burke and Raynal 1998). While it is likely that the soil laboratory method used in this study is adequate for general site characterization purposes, which was the objective in this study, the method may not provide an accurate indication of P availability within these forests. In general, the use of agricultural soil tests, such as the double acid extractable P method, for assessment of the nutrient status of forest trees has not been highly reliable due to uncertainties regarding correlations between soil extractable nutrients and tree productivity (Marschner 1986). Therefore, the live foliar tissue analyses used in this study may better reflect the nutrient status of the forests.

Distinctions between the floodplains in terms of N and P cycling are also evident when comparing litterfall N/P ratios. Use of N/P ratios provides a diagnostic tool for determining N or P limitations within live vegetation, and Koerselman and Meuleman (1996) have suggested that a critical N/P ratio in live vegetation for non-forested wetland communities is ~15. Lockaby and Conner (1999) have suggested that productivity within wetland forests reaches a maximum at N/P ratios around 12, and that ratio may represent the optimum balance between N and P within wetland forests. Ratios on both floodplains fall below the optimum balance in N and P (i.e., <12), suggesting that, particularly on the ALT, N is insufficient in relation to the amount of P available (Table 2). Lockaby and Walbridge (1998) and Lockaby and Conner (1999) predicted that wetland forests with vegetation N/P ratios below 12 would indicate N deficiency, and for the ALT floodplain, the data from this study support that claim.

Despite litterfall N/P values for the SAT floodplain falling below the threshold, SAT data do not support N-deficiency as a primary mechanism limiting vegetation production there. This becomes evident when examining the levels of N returned in litterfall, in addition to the patterns of N resorption and N NUE. Furthermore, comparisons between litter quality indices seem to support strong P limitation on the SAT. Litterfall lignin/N and C/N ratios were similar for both floodplains; however, litterfall lignin/P and C/P ratios for the ALT floodplain are much narrower than those of the SAT floodplain (Table 2). The litter quality estimates from the ALT follow patterns similar to those reported for the Ogeechee River floodplain in southeastern Georgia, where productivity was thought to be primarily N limited (Lockaby et al. 1996). In contrast, the litter quality estimates from the SAT mirror those reported by Lockaby et al. (1994) for the P deficient Little Escambia floodplain in southwest Alabama.

Differences between the two floodplains were also evident when examining N and P circulation patterns among microsites. Microsite influences on litterfall production and N and P circulation were particularly interesting for the SAT floodplain. Relationships between litterfall mass and litterfall N and P contents on the SAT floodplain indicate that production within the MPD microsites appeared to be most limited by N and P availability (Figure 1a and b). Differences in rates of N returned through litterfall among SAT microsites seemed to be driven primarily by differences in biomass production given similar litterfall N concentrations for the MPD (8,134 mg kg^{-1}) and VPD (9,052 mg kg^{-1}) microsites. For litterfall P concentrations, however, the VPD microsites (973 mg kg^{-1}) possessed significantly greater P than that of the MPD microsites (847 mg kg^{-1}). In contrast to the patterns observed for the SAT floodplain, litterfall N and P concentrations did not differ among SPD and PD microsite types on the ALT floodplain, averaging 8,647 and 1,660 mg kg^{-1}, respectively. These patterns suggest that production on the less fertile SAT floodplain was more sensitive to minor changes in nutrient availability.

Although soil exchangeable cations were significantly greater for ALT soils, the disparity between SAT and ALT floodplain soils was most dramatic for Ca. Differences in soil exchangeable-Ca, as well as exchangeable-K and Mg pools, mirror patterns observed for contrasting Southeastern (Wharton et al. 1982) and Amazonian floodplain forests (Furch 1997). The distinctions in soil Ca availability between the two floodplains reflect a differential in geochemical inputs due to differences in geology, mineralogy, and hydrology of the watersheds. The floodplains displayed strong divergence in Ca circulation in litterfall, with the SAT floodplain returning significantly lower Ca (Table 2). Relationships between litterfall mass and litterfall Ca content support the possibility of Ca-limited production on the SAT floodplain. In particular, productivity of the drier (MPD) microsites there seems to be Ca-limited (Figure 1c). However, litterfall Ca concentrations did not differ, with the ALT and SAT floodplains averaging 11,065 and 9,703 mg kg^{-1}, respectively, across both years. Therefore, lower amounts of Ca circulation in litterfall on the SAT floodplain were influenced primarily by mass.

In contrast to the patterns observed for litterfall Ca, concentrations of K in litterfall differed significantly ($P < 0.0001$) between the ALT (2,613 mg kg^{-1}) and SAT floodplains (1,955 mg kg^{-1}), suggesting that concentration influenced K return in litterfall on the SAT floodplain. Differences in K circulation and efficiency patterns between these two floodplains were also large and, for the SAT floodplain, similar to the patterns observed for P. Relationships between litterfall mass and litterfall K content on the SAT floodplain imply that K may be secondary to P in terms of nutrient limitation (Figure 1d). On the ALT floodplain, however, this relationship was not significant, suggesting that K availability does not restrain productivity on that floodplain. Additionally, K NUE patterns for the SAT floodplain indicated efficient use of K, while patterns on the ALT floodplain varied among the three-microsite types (Figure 2d).

Litterfall circulation of both Ca and K for the SAT floodplain was generally lower than that for Southeastern riverine and depressional wetland forests (Table 3). On the ALT floodplain, circulation of Ca was intermediate and was also generally low for K among wetland forest types. An exception, however, was that K circulation in litterfall exceeded that of the cypress forest stands reported by Schlesinger (1978) and Odum and Ewel (1979) (Table 3). The SAT and ALT data for K NUE are interesting in relation to values from other wetland forests in the southeastern US. Forests with the highest K NUE are the depressional cypress forests, while mixed species riverine forests appear to be the most inefficient (Table 3). Compared to these riverine forests, the SAT displays a greater efficiency of K use. The least efficient use of both Ca and K is within a 7-year-old *Populus deltoides* Bartr. ex Marsh. plantation in the Mississippi River floodplain (Nelson et al. 1987), which represents high ANPP (16.6 Mg ha^{-1} yr^{-1}) and ample nutrient availability.

In contrast to the patterns observed for both Ca and K, circulation of Mg in litterfall for the ALT floodplain was significantly lower than that of the SAT. Furthermore, rates of Mg returned in ALT floodplain litterfall were intermediate between floodplain and cypress swamp forests (Table 3). Litterfall Mg concentrations on the SAT floodplain (2,340 mg kg^{-1}) significantly exceeded the ALT floodplain (1,740 mg kg^{-1}), suggesting that differences in Mg content between floodplains may have been influenced by leaf concentration.

For the ALT floodplain, relationships between litterfall mass and litterfall Mg content were much stronger than those observed for the SAT, resulting in higher Mg NUE there. The high Mg NUE of the ALT floodplain is similar to that of depressional wetland forests; while Mg NUE values for the SAT and other riverine forests are lower (Table 3). Even though the amount of soil exchangeable-Mg on the ALT exceeds that of the SAT, increased Mg NUE on the ALT may reflect a Ca-induced Mg deficiency within the ALT vegetation.

Mass flow and diffusion are the processes by which Mg moves through the soil and is taken up by plant roots. However, Mg uptake by plant roots is dependent on several factors, including the amount of Mg in solution, soil pH, percent Mg saturation of the CEC, and clay type (Tisdale et al. 1993). High levels of exchangeable-K and Ca can also interfere with vegetation uptake of Mg (Binkley 1986). Furthermore, transport of Mg to growing tissues is characterized by slow transport within the plant (Bell and Biddulph 1963, Andrews and Siccama 1995). Therefore, increasing Mg NUE for vegetation on the ALT floodplain may be a response to the antagonistic effects of soil Ca and K availability, soil physiochemical conditions, and/or vegetation physiology.

Examining the relationships between litterfall mass and base cation contents in litterfall for the SAT and ALT provides some interesting insights into potential nutrient limitations for these two southeastern riverine forest types. The observed differences in the aforementioned relationships suggest that the array of nutrients limiting productivity on the SAT is more extensive than that of the ALT floodplain. For the SAT floodplain, ranking the relationships in order of importance based on r^2-values of regression relationships between litterfall production and nutrient content resulted in the following: P > Ca > K > N > Mg. This suggests that SAT floodplain productivity may be stimulated by first increasing P availability. However, simply increasing P availability may not solely increase production without a corresponding increase in base cation availability, particularly Ca and K. Conversely, the hierarchy of nutrients governing productivity on the ALT floodplain was as follows: Ca > Mg > N > P, while relationships between litterfall production and litterfall K content were not significant. Given the high levels of Ca circulating on the ALT floodplain, a corresponding increase in Mg availability may stimulate productivity there.

CONCLUSIONS

There is strong evidence to suggest that production on the SAT is P-limited. Circulation of P on the SAT floodplain appeared similar to patterns of temperate depressional wetland forests, which have been theorized to be P-deficient since geochemical inputs of P are typically low. The amount of P returned in litterfall for the SAT is low compared to other temperate riverine forests, and in comparison to the ALT, the SAT had higher P NUE, indicating more efficient P circulation. While the SAT litterfall N/P ratios do not suggest P limitation, the other litterfall ratios (i.e., C/P and lignin/P) and nutrient resorption of P suggest greater P limitation relative to N. Both floodplains showed similar patterns of N circulation and N NUE. However, on the ALT floodplain, the relationship between litterfall mass and litterfall N content, as well as litterfall N/P ratios, suggests that N availability plays a stronger role in limiting production on the ALT floodplain than P.

The blackwater SAT floodplain forest also showed more spatial variation in productivity and nutrient circulation. Relationships between litterfall mass and litterfall nutrient contents on the SAT were more heterogeneous for N within the drier (MPD) microsites, although this microsite type also had the lowest levels of P, Ca, and K circulation in litterfall. The MPD microsite type also circulated nutrients more efficiently than the other two SAT microsite types. The increased heterogeneity in production and nutrient circulation seems to be in response to subtle changes in nutrient availability and the sensitivity of ANPP to those changes.

As evidenced by differential patterns in base cation circulation, efforts to understand floodplain productivity should not focus solely on differences in N and P circulation. Both the SAT and ALT floodplains had high levels of Ca circulation and low Ca NUE, as well as low K circulation and high K NUE. Additionally, differences in K circulation and K NUE between floodplains indicated that K also constrains productivity on the SAT. In contrast to other temperate riverine forests, the ALT shows low levels of Mg circulation and high Mg NUE. High Mg NUE on the ALT is not a result of a lack of Mg within the system but most likely a response to the antagonistic effects of other nutrients in high supply (i.e., Ca and K).

Relationships between productivity and nutrient circulation for these two systems suggest that the array of nutrients limiting productivity in the blackwater floodplain forest was broader than those of the redwater floodplain forest. For the blackwater SAT floodplain forest, it appears that a hierarchy of nutrient limitations precedes that of N, suggesting that the nutritional needs of vegetation would first have to be met through increases in P, Ca, and K availability. The contrasting nutritional requirements of these floodplain forest types further suggest that responses to increasing anthropogenic inputs of N and P from non-point-source pollution may differ. Increasing N and/or P inputs to the blackwater SAT floodplain forest may not stimulate production unless these inputs are accompanied by higher inputs of other macroelements (i.e., K and Ca). Conversely, on the redwater ALT floodplain, increasing N inputs may result in greater rates of aboveground production given the larger soil exchangeable macronutrient pools.

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